

CHROMOSOMES OF MEXICAN SEDUM

I. ANNUAL AND BIENNIAL SPECIES

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Probably well over 100 species of *Sedum* are native to Mexico. Jacobsen (1974), whose concept of the genus is followed most closely here, listed 82 species for Mexico, but several of these probably are best reduced to synonymy. On the other hand, Jacobsen omitted some species that appear distinct, and new species are still being found at a significant rate as new areas become accessible. At least ten species of *Sedum* studied for this series of papers are considered to be new and undescribed.

Sedum is the catchall genus for the Crassulaceae, and in addition to the more "typical" species it includes a number of peculiar species that are not easily assigned to other named genera. In vegetative habit the Mexican sedums range from annuals and biennials to mostly perennials, and from delicate, minute herbs to plants that are creeping or pendulous or with sessile rosettes to bushes 2 meters or more high. With a few exceptions the floral form is reasonably constant, with 5 sepals, 5 essentially separate and spreading petals, ten stamens in two whorls, and 5 separate carpels. However, one (unnamed) biennial species is tetramerous (Fig. 19), and in other species some flowers are 6 or more parted. In some species the corolla is mostly or partly erect, spreading only in the distal half or less, and in a few species the petals are basally connate for as much as 1 or 2 mm. Two species (one of them undescribed) have only 5 stamens. In a few species the nectar scales are greatly enlarged (e.g., Fig. 19), and a few have the carpels united for a short distance at the base. Most species form inflorescences at the tips of previously vegetative stems, but some species (Section *Pachysedum*) regularly bear lateral inflorescences.

Important characters of succulent plants are not well preserved in herbarium specimens, which therefore may

provide seriously inadequate information when new species are described from them. This deficiency is compounded when the type locality is not clearly indicated or cannot be located today. Thus, identification of some plants is very difficult because descriptions of some species are inadequate, having been based on dried specimens.

In these studies about 50 different chromosome numbers ranging from $n = 7$ to $n = \text{ca. } 140$ have been found in the 90 or so species studied. Generally a rather broad concept of species has been followed, and some species, as conceived here, are variable morphologically. A good many are also variable cytologically, with two or more chromosome numbers, and one species has no less than ten numbers.

Most collections came from known localities in the wild, but many were grown in the greenhouse before study. Pressed vouchers of virtually all are in the Wiegand Herbarium or Bailey Hortorium of Cornell University. Chromosomes were studied at meiosis in conventional acetocarmine squashes of pollen mother cells. Photographs (all $\times 2,000$) are of permanent preparations.

I am particularly indebted to Dr. Reid Moran, Natural History Museum, San Diego, California, who has collected and identified many specimens. Other collections were generously provided by my colleague Professor R. T. Clausen, by Paul C. Hutchison, then of the Botanical Garden, University of California, Berkeley, and by Myron Kinnach of the Huntington Botanical Garden, San Marino, California.

For reasons of logistics and economics these counts are reported in a series of papers, rather than all in one. This first paper reports on the chromosomes of only the annual and biennial species, which are themselves rather diverse in form and chromosome number, and obviously include some species that are not closely related. Some of these species are not well known and some identifications are very uncertain. At least one is new. Still other annual and biennial species have not been available for study. I hope that the reports of the chromosome numbers here, together

with the locality data, may contribute to an eventual clarification of this poorly understood group.

The biennials usually die to the ground during the dry season (winter and spring), then look very different the second year, especially in their leaves. All biennial species have proved difficult to grow in cultivation, and this has limited direct comparison of living plants. In most cases their names and published descriptions have been based on pressed material. The authors of the species had never seen the living plants and seem not to have known whether they were annual, biennial or perennial. (Indeed, some individual plants may vary in this respect.) Jacobsen (1974) listed eight of the species reported here, three, apparently based on published descriptions, as perennials: *S. chihuahuense* (as *Villadia*), *S. flaccidum*, and *S. napiferum*. Five others were described as annual or biennial: *S. batesii* (as *Villadia hemsleyana*), *S. cormiferum*, *S. forreri*, *S. jaliscanum*, and *S. minimum*.

The species studied and their chromosome numbers are listed alphabetically in Table I; under each species collections are arranged from north to south and from west to east. The species are discussed below in geographic order, from north to south.

Table I. Collections Studied.

Sedum cf. *batesii* Hemsley $n = 31$

M10106 Oaxaca. 3 mi NW of Lachao at km 177 on road to Puerto Escondido, 1850 m (R. Moran) (Fig. 1).

Sedum cf. *chihuahuense*, Wats.

U2254 Durango. 4.5 km W of Revolcaderos, 2075 m ($n = 10$).

U2253F₁ Durango. 3 km W of Revolcaderos, 2100 m ($n = 10$).

U1657 Durango. 9 km W of Espinazo, Mex. hwy. 40. (W. Handlos 469A) (two plants both $n = 9$, Fig. 2).

U1385 Durango. 4.4 km W of Espinazo monument, Mex. hwy. 40, 2300 m ($n = 10$, Fig. 3).

Sedum cormiferum Clausen $n = 14$

SV-VG102a State of Mexico. Ravine tributary to gorge of Tenancingo R., 4 km SSE of Villa Guerrero (R. T. Clausen, from the type collection) (Fig. 4).

Sedum cf. flaccidum Rose $n = 11$

U1377 Durango. Wet flattish rocks 5 km E of La Ciudad, 2600 m (Fig. 5).

U1660 Durango. 8.5 km E of La Ciudad (W. Handlos 471A).

Sedum cf. forreri Greene $n = 8$

U1384 Durango. 12.6 km W of La Ciudad.

U1658 Durango. 11 km W of La Ciudad (W. Handlos) (Fig. 20).

M9995 Durango. La Ciudad, 2700 m (R. Moran) (Fig. 6).

U1376 Durango. 7.3 km W of El Salto.

M13332 Durango. 8 km S of El Salto, 2550 m.

U1540 Durango. Just E of Navajas, ca. 65 km W of Durango.

M13322 Durango. Navios, 59 km W of Durango, 2300 m (R. Moran).

U1374 Durango. Mex. hwy. 40 at km 55 marker W of Durango city, 1.9 km W of Tepalcates, 2550 m.

Sedum jaliscanum S. Wats.

U1396 Zacatecas. Juchipila Canyon, 7 km S of Moyahua, km 99 N of Guadalajara, 1100 m ($n = 18$).

U1400 Jalisco. 5.5 km E of Ayo el Chico. ($n = 24$ prob).

U2142 Jalisco. In barranca at km 18 N of Guadalajara, 1300 m (probable topotype). ($n = 18$, Fig. 9).

U2114 Guanajuato. Picachos de la Bufa, NE of Guanajuato city, 2300 m ($n = 18$).

U2259 Michoacán. 7 km W of Zacapu, 2200 m, on lava. ($n = 11$, Fig. 7).

- U2137 Michoacán. Km 49 on Pátzcuaro road, 14 km E of Uruapan, on lava. ($n = 34$, Fig. 14).
- U1405 Michoacán. Mex. 37 at km 94, 19 km S of Uruapan, 1280 m ($n = 34$).
- U1415 Michoacán. Sierra de Ozumatlan, 32 km E of Morelia. ($n = 20$, Fig. 10).
- U2266 Michoacán. 7.5 km S of Zinapécuaro, 2080 m ($n = 23$, Fig. 12).
- U2264 Michoacán. 1 km N of Huajúmbaro, 2250 m ($n = 25$, Fig. 13).
- U2262 Michoacán. 3.2 km SE of Huajúmbaro, 2380 m ($n = 25$).
- U1426 State of Mexico. Below Presa Tilostoc, S of Valle de Bravo ($n = 17 \pm 1$).
- U1737 State of Mexico. Barranca de Ahuatenco. (R. Moran). ($n = 20$).
- U1445 Guerrero. Taxco. ($n = 16$, Fig. 8).
- SV-T17 Guerrero. N Side of Taxco (R. T. Clausen). ($n = 16$).
- U1434 Morelos. 1.5 km W of Tepoztlán. (Topotype of *S. naviculare* Rose). ($n = 21$, Fig. 11).

Sedum minimum Rose $n = 11$

- U1470 Hidalgo. Meadow in fir forest, 2 km N of Pueblo Nuevo, El Chico Natl. Park, 3000 m (Fig. 15).

Sedum napiferum Peyritsch $n = 11$

- U1422 State of Mexico. Flattish rocks on W spur of hill N of Toluca, 2750 m (Fig. 16).
- #5 Same locality (R. T. Clausen).

S. cf. vinicolor S. Wats. $n = 7$

- M21964 Sonora. 6 km NW of Yécora, 1525 m (R. Moran) (Fig. 17).

S. sp. $n = 22$

- U1381 Durango. Puerto Buenos Aires, 9 km W of La Ciudad, 2700 m.
- U1659 Same locality (W. Handlos) (Fig. 18, 19).

The northernmost collection, *Sedum* cf. *vinicolor* S. Wats., is a fibrous-rooted annual about 10 cm high, much branched at and near the base, with stems and leaves marked with many tiny wine-colored spots, probably depending partly on exposure to sun. The sepals are green, rather thick and spreading, a little shorter than the corolla. The petals are pale greenish yellow in the distal half, increasingly marked toward the base with wine-colored spots, usually in transverse bands. The filaments and pistils are heavily spotted with the same color. The plants resemble *S.* cf. *forreri* from farther south, but the petals are narrower and yellowish in background color (vs. white in cf. *forreri*), and the carpels do not become as widely spreading. This species has the lowest chromosome number ($n = 7$, Fig. 17) yet found in more than 200 species of Mexican Crassulaceae studied (Uhl, 1970; Uhl and Moran, 1973; Uhl, unpublished). The plant came from near Yécora, Sonora, near the Chihuahua border and probably less than 100 km from the type locality of *S. vinicolor* (Norogachi, Chihuahua) but more than 1000 meters lower.

The next four species were collected along or near the highway (Mex. 40) from Durango to Mazatlan, which provides the only good access to the vast Sierra Madre Occidental. The genus is very poorly known in this area, and the identifications from here also are only tentative.

Sedum sp., a small napiform biennial with very pale greenish tetramerous flowers and conspicuous brownish nectaries (Fig. 19), is very distinctive and certainly an undescribed species ($n = 22$, Fig. 18). It was found only at Puerto Buenos Aires, 9 km west of the sawmill town of La Ciudad and 154 km west of Durango city.

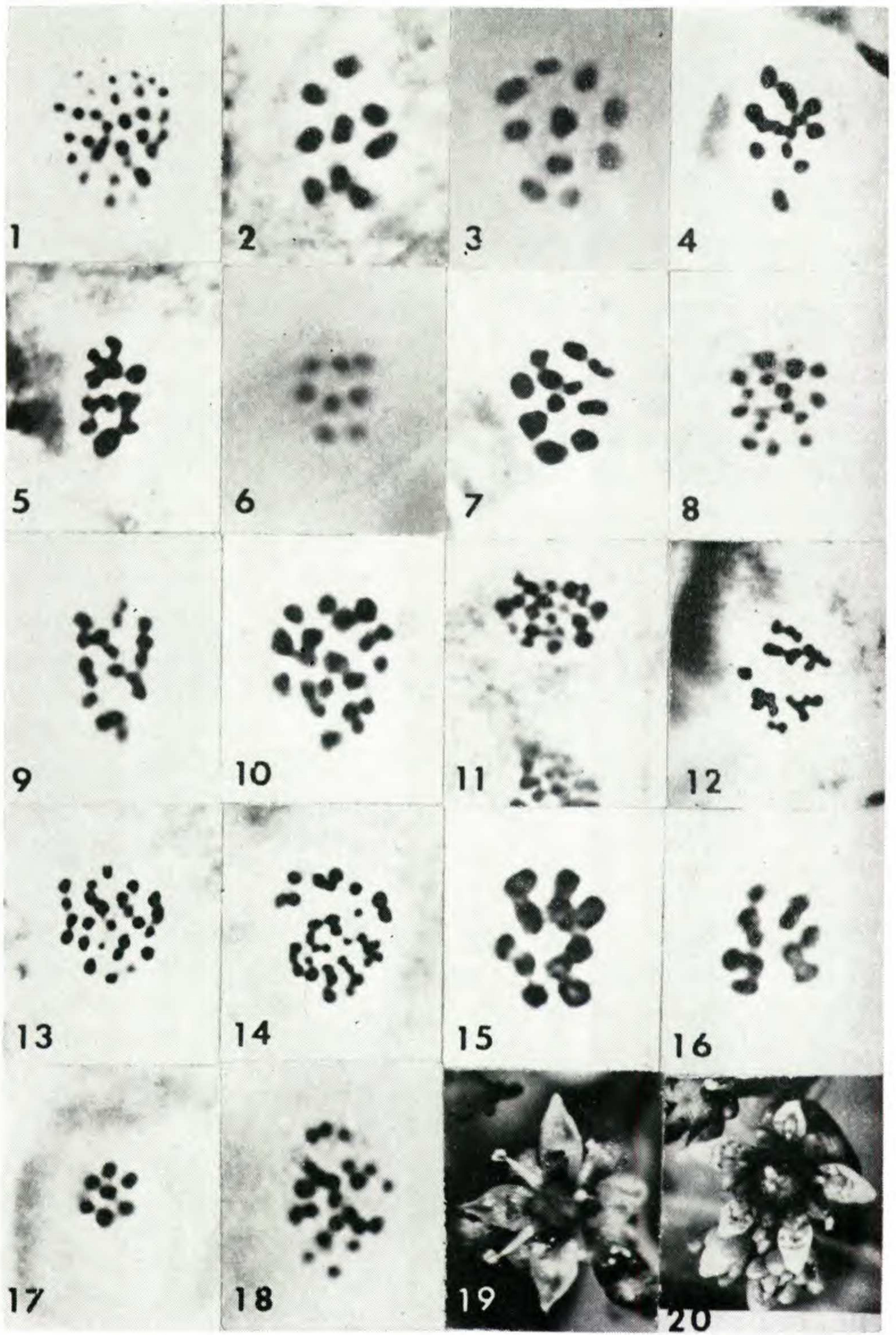
Sedum cf. *forreri* Greene is a fibrous-rooted annual with leaves and stems usually strongly flushed with red and with white petals cross-banded with red (Fig. 20; $n = 8$, Fig. 6). It occurs at many rocky places along the road from 55 km west of Durango for about 100 kilometers westward, to west of Puerto Buenos Aires. The type locality of *S. forreri* is vaguely given as the "higher Sierra Madre, back

of the city of Durango" at 8100 feet, and the petals are described as white or faint rose color.

Sedum cf. *flaccidum* Rose is a napiform biennial (?) with flowers similar to those of *S.* cf. *forreri* in coloring, found on open, wet, flattish rocks at two places a few kilometers east of La Ciudad. *S. pringlei* S. Wats. is possibly an older name for the same species. The type locality of *S. flaccidum* is Tejamén, Durango, about 135 km NE of La Ciudad, whereas *S. pringlei* was described from Cusi-huiríachic, Chihuahua, more than 500 km to the north. Whatever its name, its morphology, habitat and chromosome number ($n = 11$, Fig. 5) suggest a relationship with *S. napiferum* and *S. minimum* of central Mexico.

Sedum cf. *chihuahuense* S. Wats. ($n = 9$ and 10 , Figs. 2, 3), the fourth species of the Durango-Mazatlán road, was found in clefts in steep rock at many places from Espinazo del Diablo (22 km west of La Ciudad) westward for 35 kilometers and into Sinaloa. It is biennial with narrowly oblanceolate leaves the first year, forming a small corm, and the second year producing cymes with small white flowers. This species is quite reminiscent of *S. jaliscanum* of central Mexico, but its first-year leaves are not spatulate.

Sedum jaliscanum S. Wats. is broadly conceived here, following Clausen (1959). It is by far the most widely distributed, occurring in rock crevices often in lava in eight states, from Morelos westward across volcano-studded central Mexico to Nayarit. It is also the most variable of the annual and biennial species studied, both morphologically and cytologically. Clausen found statistically significant differences in 14 of 18 characters among plants from six different localities, but he considered them all the same species. In 16 collections studied at least eight different chromosome numbers were found, ranging from $n = 11$ to $n = 34$ (Fig. 7-14). The type locality is near Guadalajara, where $n = 18$ was found (U2142, Fig. 9). A topotype of *S. naviculare* Rose, reduced to *S. jaliscanum* by Clausen (1959), had $n = 21$ (U1434, Fig. 11). In most collections, especially those with $n = 34$ (Fig. 14), (but not in those



with $n = 18$) the chromosomes differ substantially in size, a rather unusual condition in *Sedum*.

Sedum jaliscanum is widespread as disjunct populations in a rugged volcanic area that is remarkably variable and that must have experienced frequent and drastic changes in local environments. On the one hand, volcanic activity and fluctuations in available moisture during alternate pluvial and dry periods (presumably coinciding with glacial advances and retreats on the higher summits and farther north) must have repeatedly fragmented, decimated, or exterminated earlier populations of the species. On the other hand, the same changes provided new and favorable habitats elsewhere. Over a long period of time numerous colonizations and recolonizations of newly suitable areas must have occurred. These conditions, together with the short biennial generation time, provided a great many chances for new and different chromosomal types to occur and to become fixed. Stebbins (1974, pp. 158-159) pointed out that great chromosomal diversity is found in many groups of herbaceous plants in pioneer habitats of this sort, and he attributed this probably to "selective pressure for linked gene combinations". The favored combinations are not the same in all populations because differences in the environment may favor different gene linkages and different chromosomal arrangements and number.

Figs. 1-18: Chromosomes at metaphase I in pollen mother cells, $\times 2000$. Fig. 1: *S. cf. batesii*, M10106, $n = 31$. Fig. 2: *S. cf. chihuahuense*, U1657, $n = 9$. Fig. 3: *S. cf. chihuahuense*, U1385, $n = 10$. Fig. 4: *S. cormiferum*, SV-VG102a, $n = 14$. Fig. 5: *S. cf. flaccidum*, U1377, $n = 11$. Fig. 6: *S. cf. forreri*, M9995, $n = 8$. Figs. 7-14: *S. jaliscanum*. Fig. 7: U2259, $n = 11$. Fig. 8: U1445, $n = 16$. Fig. 9: U2142, $n = 18$. Fig. 10: U1415, $n = 20$. Fig. 11: U1434, $n = 21$ (metaphase II). Fig. 12: U2266, $n = 23$. Fig. 13: U2264, $n = 25$. Fig. 14: U2137, $n = 34$. Fig. 15: *S. cf. minimum*, U1470, $n = 11$. Fig. 16: *S. napiferum*, U1422, $n = 11$. Fig. 17: *S. cf. vinicolor*, M21964, $n = 7$. Fig. 18: *S. sp.*, U1659, $n = 22$. Fig. 19: Flower of *S. sp.* (U1659), $\times 4$. Fig. 20: Flower of *S. cf. forreri* (U1658), $\times 2.5$ (millimeter scale).

The highest chromosome number in *S. jaliscanum*, $n = 34$ (Fig. 14), is more than three times the lowest number, $n = 11$ (Fig. 7). However, the size of the chromosomes seems to vary inversely with their number, and the aggregate amount of chromosomal material appears not to differ much. This observation and the presence of so many intermediate numbers suggest that the variation in chromosome number may be sufficiently accounted for by dysploidy, i.e., by evolutionary rearrangement of essentially similar genetic material into different numbers of chromosomes, with no polyploidy involved. Dysploidy is common in the Mexican Crassulaceae, including *Sedum*, but in no other Mexican species has it developed to this extent.

An apparently parallel situation occurs in the similarly polymorphic *S. polytrichoides* of Japan and South Korea, which exhibits a similarly wide range of 13 different chromosome numbers, from $n = 11$ to $n = 35$ (Uhl and Moran, 1972). Calculations of nuclear volume in *S. polytrichoides* showed no correlation with chromosome number, suggesting dysploidy, probably with no polyploidy.

Sedum minimum ($n = 11$, Fig. 15) is known from only three localities, each with perhaps a different subspecies (Clausen, 1959). Stoutamire and Beaman (1960) reported $n = 10$ in *S. minimum* from Nevado de Toluca, the type locality. The material studied here came from Pueblo Nuevo, Hidalgo, a population that Clausen (1959, p. 303-304) considered possibly a different subspecies or even species.

Sedum napiferum ($n = 11$, Fig. 16) is known from only one locality, just north of Toluca. Clausen (1959) considered it closely related to *S. minimum*, and this view is supported by the similarity of their chromosomes. *S. cf. flaccidum* (above) occurs in similar habitats (wet, flattish rocks) along the Durango-Mazatlán road. It is similar to these two morphologically; it also has $n = 11$, and it probably is related.

Sedum cormiferum ($n = 14$, Fig. 4) was studied from a plant of the type collection, and its only known locality. Clausen (1959) considered the species most closely related to the perennial *S. clavifolium* ($n = 34$ prob.).

Sedum cf. *batesii* ($n = 31$, Fig. 1) of the Sierra Madre del Sur "is most closely related to *S. jaliscanum*" ($n = 11$ to $n = 34$) of central Mexico (Clausen, 1959, p. 289). Together with *S. cf. chihuahuense* ($n = 9$ and 10) of northwestern Mexico, these three may comprise a second group of related biennial species.

Chromosome numbers found in more than 200 species of Mexican Crassulaceae that have been studied include every number from $n = 7$ to $n = 36$, as well as many higher numbers (Uhl, 1970; Uhl and Moran, 1973; Uhl, unpublished). It is noteworthy that the three lowest numbers ($n = 7$ to $n = 9$) are known only in the annual and biennial species of *Sedum* reported here, along with several species having $n = 10$ or $n = 11$. The lowest number known in a perennial species is $n = 10$ in an undescribed *Villadia* (Uhl, unpublished).

SUMMARY

Chromosome numbers are reported for ten annual and biennial species, including one undescribed species and several others not certainly identified. *S. cf. flaccidum*, *S. minimum*, and *S. napiferum* are similar morphologically and all have $n = 11$. At least eight different numbers from $n = 11$ to $n = 34$ were found in the widespread and polymorphic *S. jaliscanum*, with the chromosomal variation attributed probably to dysploidy, rather than to polyploidy. *S. cf. chihuahuense* ($n = 9, 10$) and *S. cf. batesii* ($n = 31$) may be related to *S. jaliscanum*. *S. cf. vinicolor* has $n = 7$, the lowest number known in the Mexican Crassulaceae, and the related *S. cf. forreri* has $n = 8$. *Sedum cormiferum* has $n = 14$, and an undescribed species has $n = 22$.

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